EFFECTS OF SEASON, SEX, AND DIETARY NITROGEN ON MUSKOXEN

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ABSTRACT

Growth and survival of muskoxen (*Ovibos moschatus*) are dependent on forage that varies in quality and quantity. One of the most limiting factors is nitrogen. In chapter 1, I predicted that growth would vary with season, sex and dietary nitrogen. While growth is highly seasonal and results in dimorphism, it is not affected by supplemental nitrogen. In chapter 2, I predicted an inverse relationship between intake and digestibility of diets in adults. Intakes increased dramatically from spring to summer with no impact on digestibility. This resulted in increased body fat from summer to winter with little change in body protein. Cellulose digestibility decreases in winter, suggesting a seasonal regulation of digestive and absorptive systems. High solute loads did not affect plasma osmolality because renal function probably eliminates excess N and K during autumn. Differences in intake and growth patterns are probably the result of sexual and non-sexual hormonal controls.

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INTRODUCTION

All animals have a limited amount of time in which to complete the tasks of birth, growth, reproduction, and rearing of young. The faster an animal can reach a reproductive size, the earlier it can reproduce, and ultimately the more offspring it can produce throughout its lifetime, thus maximizing fitness.

The most common constraints on diet quality are usable energy content and nitrogen content. Ruminants have overcome the indigestibility of most plant components through the symbiotic association with microbes. These microbes aid them in breaking down the fiber matrix of plants. However, large proportions of slowly degrading plant material along with defense mechanisms such as secondary compounds can limit the amount of metabolizable energy available from a given plant species during a given amount of time. The energy gain from plants can change depending on time of year. Plants are more nutritious during the spring and summer when the ratio of cell wall to cell solubles is low and become less nutritious as senescence occurs. Protein is quite often low in this system, and the amount available follows this same general trend. Protein is comprised of 16% nitrogen. Nitrogen, including non-protein nitrogen, is often utilized by microbes before it becomes available to the animal. Nitrogen can be used to build microbial protein or it may be given off as ammonia. Ammonia can be taken up by the animal and converted to urea, after which it is either filtered out through the kidneys or dumped back into the rumen for use by the microbes. Therefore the possibility of urea recycling exists in ruminants.

The quality and quantity of forage in the circumpolar arctic is highly seasonal. Arctic summers are short, and plant species have a very limited time to grow and produce seeds. These plant species senesce and the nutritional quality of the forage rapidly declines. In addition, the arctic is snow covered for most of the year, thereby making the forage less available and more difficult to obtain. These constraints add to the energetic cost of foraging. Animals on highly seasonal forage can compensate for the changes in quality and quantity by maximizing intake and growth when conditions are favorable, and minimizing energy requirements when forage becomes less available.

Muskoxen (*Ovibos moschatus*) are one of only two ungulates to successfully colonize the arctic. Mature muskoxen derive most of their energy from fermentation of the fiber matrix in plants (Adamczewski et al. 1994a; 1994b). Stores of energy as fat are depleted by inadequate food intake, high thermal demands and fetal growth in winter and by demands for early lactation in spring (Parker et al. 1990; Adamczewski et al. 1997; Rombach 2001). The energy requirements for maintenance of body tissues follow this seasonal trend (Lawler and White 1994; Nilssen et al. 1994).

Muskoxen are non-migratory animals that spend most of the winter months inactive and resting, thus lowering their energy requirements. However, the pattern of protein demands may differ from those of energy. Protein demands would be high in midwinter for fetal growth in the third trimester of pregnancy (Barboza and Bowyer 2000), during early spring for lactation (Parker et al 1990) and through late summer for growth of hair (Flood et al. 1989) and any net gain of lean mass. However, it is not clear how these ruminants metabolize nitrogen and body protein on diets of very low N content

that often limits production of domestic livestock (Annison and Bryden 1999).

The intentions of these studies were to determine patterns of growth, lean mass and fat deposition throughout a year, and to determine the extent that protein may limit production in growing and mature muskoxen. If supplementing dietary protein in excess of a base diet resulted in improved growth of lean tissues and/or hair, how effective would protein supplementation be and at what point in time during the year would that extra protein be utilized?

CHAPTER 1

Climate and weather influence the growth of ungulate populations at high latitudes either by direct effects on precipitation or by indirect effects on the plants they consume (Forchhammer et al. 2001; Post and Stenseth 1999). The sensitivity of plants and herbivores to climate change reflects the brief season of annual plant growth at high latitudes when high temperature and long photoperiod prevails during a short summer (Lenart et al. 2002). Ungulates are therefore presented with foods of increasing diversity, quality and abundance in summer (Klein and Bay 1990; Klein and Bay 1994; Thing et al. 1987). Autumnal senescence reduces the quality of plants for ungulates, while wind and snow may further reduce the availability of these forages through winter (Forchhammer and Boertman 1993; Ihl and Klein 2001; Nelleman 1997; 1998).

Muskoxen (Ovibos moschatus) are the largest grazers in the circumpolar arctic (Klein 2000). Although wild herds consume a variety of forages, their diet is mainly comprised of sedges and grasses that are high in fiber and low in sources of nitrogen (N) such as protein (Forchhammer 1995; Larter and Nagy 1997; Nelleman 1998; Schaefer and Messier 1996). Consumption of legumes and dicotyledonous plants (Mulder and Harmsen 1995) may however, supplement intakes of N from graminoid plants especially among females and growing subadults (Forchhammer 1995; Forchhammer and Boomsma 1995; Oakes et al. 1992). Growth of muskoxen may be influenced by the abundance and

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quality of forages available in the small home ranges used by mixed herds. This suggestion is supported by high rates of recruitment of young animals into the breeding population when muskoxen were introduced to new ranges in Alaska (Reynolds 1998) and Canada (H naff and Cr te 1989). Furthermore, muskoxen from areas of low forage abundance in East Greenland are smaller in size and begin breeding at an older age when compared with herds on higher quality ranges to the west (Olesen et al. 1994).

Although the availability of energy and nutrients can limit mass gain in northern ungulates, growth rate is also affected by endogenous controls associated with season and sex (Price and White 1985). Growth of caribou and reindeer (*Rangifer tarandus*) follow a seasonal pattern with the lowest mass gain in winter (Leader-Williams and Ricketts 1981; McEwan 1968). Similarly, growth of muskoxen may follow annual patterns of activity (Cot et al. 1997; Schaefer and Messier 1995; 1996), food intake (Adamczewski et al. 1994a), basal energy expenditure (Lawler and White 1997; Nilssen et al. 1994), and hair growth (Flood et al. 1989) that are lowest in winter.

Sexes may however, differ in the pattern and cost of growth because adult males are 25% larger than females among muskoxen (Klein 2000). Fitness of males increases with body size whereas early maturation and onset of breeding is most advantageous to long-lived females in polygynous mating systems (Reiss 1989; Green and Rothstein 1991; Gaillard et al. 2000). Differences in body size between the sexes may reflect prolonged growth in males (Jarman 1983) as well as attenuated growth and early reproduction in females, both of which may be enhanced by changes in climate and forage production at high latitudes (Post et al. 1999).

We describe a study of captive muskoxen that tests the effect of diet quality on growth from weaning to 3 y of age when both sexes can reproduce. Muskoxen were fed grass hay with supplements of either medium or high N content to provide two diets of similar composition to forages consumed in the wild. We tested the hypothesis that size dimorphism is the result of a higher rate of growth in males than females. We measured changes in body composition to test the hypothesis that mass is gained as both fat and lean tissue during summer. We predicted that the high N supplement would increase mass gained as lean tissue and hair when compared with the medium N diet.

MATERIALS AND METHODS

We studied nine muskoxen (*Ovibos moschatus*) (5 male: 4°female), at the R. G. White Large Animal Research Station (Fairbanks, Alaska, USA; 65°N 146°W) under protocol #00-003 approved by the Institutional Animal Care and Use Committee. Seasons at this latitude are described as follows: early winter = October to January, late winter = February to April, spring and summer = May to July, and autumn = August to September. These periods correspond to the annual reproductive cycle of the herd, that is, breeding or rut in autumn, gestation through winter and parturition at the start of spring.

Body mass was recorded on the same day each week (± 0.5 kg Tru-Test Model 703 scale; San Antonio, TX) from weaning in October 1999 (age 139 days) to March 2001 (age 669 days). Animals were held in a common enclosure and provided with water ad libitum as fresh water or snow. Fresh grass (*Bromus* sp.) was available without access to browse or other forages during the summer. Brome grass was also provided ad libitum

as hay throughout the year.

Supplements were based on cereal grains (e.g. barley and corn) and ground roughage (e.g. alfalfa and beet pulp) mixed with mineral and vitamin premixes and prepared as pellets (Alaska Pet and Garden, Anchorage Alaska). Three supplements were used in this study: a common supplement was fed from weaning (139 days) to 309 days of age°(March 2000) when animals were ranked by size and switched to either a medium N supplement or a high N supplement. Supplements were provided at 70 $g/kg^{0.75}$ each week in three equal rations on the basis of average body mass for the previous week. Rations of all supplements were readily consumed. Animals were separated and supervised during feeding of supplements to prevent dominance behavior and any departures from the prescribed ration. Protein sources for both supplements included corn, barley and alfalfa. Fishmeal was included only in the high N supplement to provide a high quality source of protein that could bypass ruminal fermentation (Van Soest 1994). Fishmeal also increased enrichment of the diet with ^{15}N and provided a label for monitoring the fate of absorbed N in blood and hair.

Proximate analyses of the diets (Table 1.1) were performed with procedures described by Barboza and Jorde (2000). Dietary crude protein (CP) was calculated from total N content on the basis of 6.25 gCP/gN (Robbins 1993). Daily intakes of growing muskoxen can be calculated from the rate of supplementation (70 $g/kg^{0.75}$ per week or 10 $g/kg^{0.75}$ per day) and the dry matter intakes of eight nonreproductive adult males fed the same hay and supplements in summer (75 $g/kg^{0.75}$) and late winter to spring (46 $g/kg^{0.75}$; Peltier et al. unpublished data). Daily consumption of N for muskoxen of 50 kg body

mass was estimated at 1.21 $gN/kg^{0.75}$ and 0.79 $gN/kg^{0.75}$ in summer and winter respectively for hay and the common supplement. Estimated daily intakes for 100 kg animals in summer was 1.10 $gN/kg^{0.75}$ for hay with the medium N supplement, and 1.51 $gN/kg^{0.75}$ for hay with the high N supplement. Daily intakes in winter for 100 kg animals were estimated at 0.67 $gN/kg^{0.75}$ for the medium N supplement and 0.93 $gN/kg^{0.75}$ for the high N supplement combined with hay. These intakes would provide 1.46 %N (9.1 %CP) and 2.02°%N (12.6 %CP) in dry matter ingested as hay combined with supplements of medium N and high N respectively.

Growth rate was determined as the difference in mass between the start and end of each period divided by the number of days in the period. Body composition was determined by water dilution (^3H_2O) in the spring, when animals were switched from a common supplement to either the medium N or the high N supplement (312 days of age). Body composition was also measured in autumn at the midpoint of the experiment (522 days), and in the following spring at the end of the experiment (668 days). Intractability of two animals precluded dosing with labeled water and resulted in only seven animals receiving doses at 522 and 668 days of age. Each animal received a single intra-jugular dose of tritiated water at 1.80 µCi/kg body mass (133.31 µCi/g ^3H_2O in 0.9% NaCl solution; Sigma Chemicals, St. Louis, MO). All animals were held in covered pens without access to drinking water, snow or food for 3 h to allow equilibration of the dose with body fluids. Blood was sampled from the jugular vein into dry heparinized tubes (Becton, Dickinson, Rutherford, NJ) before dosing and at 3, 6 and 24 h from the dose. Plasma was separated at 300 x g in a bench centrifuge and stored at -20°°C. Samples were

assayed for ^{3}H by scintillation counting and corrected for quench and background counts (Beckman LS6000SE, Beckman Instruments Inc. Redmond WA).

Body water space (W) was calculated from the concentration of ^{3}H in plasma at 3 h from dosing as: W (kg) = [Dose (dpm) Equilibration (dpm/mL)] x 1000 (mL/kg). The dose was equilibrated by 3 h because counts of H^{3} (dpm/mL) in blood declined linearly from 3 to 24 h, and because water space calculated from the intercept of the regression (concentration at zero time) was similar to that calculated from the concentration in blood at 3 h. Water space was corrected for water in the digestive tract with the assumption that ingesta contained 84.13 % water, and that ingesta was 18 % of body mass as measured in adult muskoxen from this population (Barboza and Blake unpublished data). Ingesta free mass of the body (IFM) was calculated from body mass (BM) as: IFM (kg) = BM - (BM * 0.18). Therefore net water space (NW) associated with lean tissues was calculated as: NW = [W * 0.9] - [0.8413 x (BM -IFM)]. This calculation assumes that $^{3}H_2O$ space overestimates water space by 10 % (Chan-McLeod et al. 1994; Fancy et al. 1986). Lean mass (NM) was subsequently calculated on the basis of 68.62% water (Gerhart et al. 1996) as: NM = NW 0.6862. Lipid mass (LM) was calculated as the difference between lean and ingesta free mass as: LM = NM - IFM.

Subcutaneous fat was measured via ultrasound (– 0.1cm; Technicare Model #SSD-210DX, Denver, CO) on the rump at the midpoint of a transect extending from the iliac crest to the ischial tuberosity (Stephenson et al., 1998; Rombach 2000) in autumn (522 days) and in the following spring (668 days). Stature was measured in a vertical distance from the floor across the top of the shoulders and across the top of the rump.

Hair was sampled by shaving approximately 25 cm^2 on the right shoulder in autumn (522 days). Samples were dried to constant mass at 55¡ C to calculate density (mg/cm^2) on the basis of dry matter. Underwool (qiviut) was subsequently analyzed in an elemental analyzer (LECO CNS2000, LECO Corp., St. Joseph, MI) for nitrogen and sulfur. Samples of blood, hair, and food were also analyzed for ^{13}C and ^{15}N enrichment by isotope ratio mass spectrometry (Europa Scientific 20-20 Continuous Flow IRMS, Europa Scientific, Chestershire, UK). Enrichments were expressed as δ (ppt) against air (^{15}N) or Pee Dee Belemnite (^{13}C; Wolfe 1992).

We used ANOVA to test effects of sex, diet, tissue and time with SYSTAT 10.0 (SPSS Inc. Chicago, IL). Repeated measures within the same animal were used to test the effect of time on body mass, body composition and stature. Repeated measures of tissues were used to compare isotopic enrichment within animals. Statistics were analyzed and considered significant at $P < 0.05$. Pairwise contrasts were performed with Bonferroni s adjustments for multiple comparisons. Results are reported as means with one standard deviation (– SD).

RESULTS

Males were larger than females from 309 days old (Fig.˚1.1) to the end of the study. However, growth rates were not significantly different between sexes through the first winter and into spring and summer. Males gained mass more rapidly than females in autumn at 474 days of age (0.29 ± 0.07, vs. 0.15 ± 0.05 g/d) but returned to a similar rate of growth as females in the second winter (Fig. 1.2). Although males were heavier than

females, stature did not differ with respect to diet or sex ($P > 0.05$) in either autumn (rump 87 – 2 cm; shoulder 92 – 5 cm) or winter (rump 93 – 4 cm; shoulder 95 – 6 cm). Body mass gained from spring (312 days) to the second winter (669 days) was comprised of water and lean tissues as well as fat (Fig. 1.3). Lean mass was conserved (86°– 21 kg to 92 – 12 kg) over the second winter (522 to 669 days; $P > 0.05$; Fig. 1.3). Body fat content was low during the first year (1.4 ± 3.3 %) but increased to 16.5 ± 7.7 % of body mass in the second year.

Supplemental N did not affect body mass ($P = 0.530$), rates of mass gain ($P = 0.250$), or body composition measured by water dilution ($P > 0.05$). Although total fat was similar between diets at 522 days of age, subcutaneous fat at the rump was deeper in animals on the high N supplement than those fed the medium N diet (Fig. 1.4). This difference in subcutaneous fat diminished over winter to similar depths between diet groups in spring (Fig. 1.4).

Nitrogen supplementation did not affect either density (99 mg/cm^2) or composition (16 % N, 2.9 % S) of hair. Although diets differed in enrichment of ^{15}N (6.4 ppt for high N vs. 1.8 ppt for medium N), hair was similar in enrichment between diet groups ($P > 0.05$; Fig. 1.5a). Enrichment of plasma and erythrocytes with ^{15}N were however, greater for animals fed the high N supplement than for those fed the medium N diet. Grass hay was depleted in ^{13}C compared to both supplements, which were similar in enrichment of C (Fig. 1.5b). All tissues were more enriched in ^{15}N and ^{13}C than hay. Enrichment of plasma with both ^{15}N and ^{13}C differed between autumn and spring (Fig. 1.5).

DISCUSSION

The first hypothesis that growth rate determined size dimorphism in muskoxen was not supported by measures of stature but was supported by mass gained during the second summer (Fig. 1.2). Mass gains of captive muskoxen declined between summer and winter even though hay was provided ad libitum. Winter depression of body mass and growth in northern ruminants has been related to the effects of short day length on growth hormone, thyroid hormones (Ryg 1983; Ryg and Langvatn 1982) and insulin like growth factor (Suttie and Webster 1995). These declines in mass or growth may be associated with reductions in food intake and digestive function mediated by melatonin (Domingue et al. 1992; Eloranta et al. 1995). Reductions in concentrations of thyroid hormones in plasma, basal metabolic rate (Lawler and White 1997; Nilssen et al. 1994), and food intake (Adamczewski et al. 1994a; White et al. 1984) of muskoxen during winter are consistent with an effect of short photoperiod on growth. Seasonal changes in ^{15}N and ^{13}C enrichment of plasma in both groups of growing muskoxen probably reflect changes in both rates of food intake and metabolism over winter (Fig. 1.5b).

Differential mass gains in muskoxen may also reflect attenuation in seasonal growth of females compared with males (Fig. 1.1; 1.2). Polygyny is associated with prolonged growth of males compared with females in several mammals (Jarman 1983) including northern ungulates such as moose (Spathe et al. 2001) and reindeer (Leader-Williams and Ricketts 1981). Smaller body size of females may be advantageous to lifetime reproductive success if curtailed growth facilitates earlier breeding (Green and

Rothstein 1991; Karubian and Swaddle 2001). Early maturation in bison (*Bison bison*) results in reduced growth and infertility the year after first parturition, but early maturing females produce more offspring over their lifespan than other females (Green and Rothstein 1991).

Although female muskoxen do not usually give birth until their third year (Klein 2000), animals on a high plane of nutrition will enter estrus and reproduce at 2 years of age in captivity (White et al. 1997) and in the wild (Jingfors and Klein 1982; Reynolds 2001). Secretions of reproductive hormones such as estrogen in autumn may underlie sexual differences in growth (Lawrence and Fowler 1997) but the specific effects of hormones on food intake and metabolism awaits direct confirmation from measures of gonadal development and endocrine function (Owens et al. 1993; National Research Council 1994) during growth of northern ungulates.

Compositional changes underlie seasonal mass gains in growing muskoxen. Body mass gains of muskoxen were primarily due to lean tissue during the first year, which probably reflects musculoskeletal growth (Heinrich et al. 1999). Average fat content of muskoxen at 312 days of age was only 1.4 % of body mass which is similar to growing caribou (*Rangifer tarandus*; 1.4-2.3 %; Reimers et al. 1982; Gerhart et al. 1996) and yearling muskoxen from the wild (7 %; Adamczewski et al. 1995). Although gains in limb length may benefit mobility in deep snow, the lack of large fat reserves over the first winter could contribute to mortality of young muskoxen (Larter and Nagy 2001a). Maternal supplies of energy and nutrients in milk may offset low fat reserves of young muskoxen during the first winter because weaning may be delayed until the end of winter

(Thing et al. 1987; Parker et al. 1990). Growth over the second year resulted in similar deposits of body fat (16.5 % of body mass) to adult females in the wild (11.6-13.9 % of body mass; Adamczewski et al. 1995), which suggests that captive females could establish sufficient reserves of fat to sustain pregnancy in their second year (Adamczewski et al. 1998).

The conversion of dietary protein to fat or lean tissues is indicated by the isotopic enrichment of ^{15}N and ^{13}C in growing muskoxen. We estimated that grass hay provided 76 % and 53 % of dietary N for animals fed medium N and high N supplements respectively. Enrichment of tissue N above dietary hay and the medium N supplement suggests that N enters several pathways that select for the heavier isotope (Fig. 1.5a). It is likely that these pathways include microbial systems in the digestive tract and endogenous systems within the organs and cells of the animal (Gannes et al. 1997; 1998). Although utilization of dietary protein by ruminal microbes will result in N being absorbed by the animal as ammonia or as microbial amino acids, dietary proteins that bypass microbial fermentation could be absorbed as amino acids without modification (Annison and Bryden 1999). Proteins in the high N supplement included those from fishmeal that often bypasses ruminal fermentation (Van Soest 1994). If proteins in the high N supplement were absorbed and incorporated as amino acids we would expect to see elevated $\delta^{15}N$ in the tissues. Although tissue $\delta^{15}N$ was consistently higher in animals fed the high N supplement than those fed the medium N diet, enrichments of N in hair were similar between groups. This suggests that N absorbed from the supplements were not preferentially incorporated in hair even though supplementation covered the entire

period of seasonal growth of underwool from May to November (Flood et al.1989). Differences in hair $\delta^{15}N$ between the groups could be ameliorated by a greater effect of endogenous or microbial fractionation of the medium N supplement than the high N supplement but this suggestion requires confirmation from direct measures of N kinetics in northern ungulates.

The conversion of excess dietary protein to fat is consistent with greater depths of subcutaneous fat in muskoxen fed the high N supplement than those fed the medium N diet (Fig. 1.4). Maximum rates of protein deposition in lean tissues and in hair are ultimately controlled by genotype but modulated by several hormones (Breier et al. 2000; Owens et al. 1993) and by the rate of protein synthesis in each organ (Adams et al. 2000). Dietary supply of sulfur amino acids can limit hair growth in domestic ruminants (Black and Nagorcka 1993) but estimated dietary content of S fed to growing muskoxen (0.17-0.20 % of dry matter) was similar to those required by domestic goats, sheep, and cattle (National Research Council 1981; 1985; 2000). Changes in composition of hair with age and sex of muskoxen (Rowell et al. 2001) suggest that the requirement and timing of protein and sulfur deposition may vary between males and females depending upon reproductive state (Barboza and Bowyer 2001).

The hypothesis that lean mass gains of muskoxen would increase with supplemental dietary N was not supported by measures of stature, body composition, or hair density. This suggests that N supplied by hay and medium N supplement (9.13 % CP of dietary dry matter) at daily rates of 672 $mgN/kg^{0.75}$ in winter, and 1095 $mgN/kg^{0.75}$ in summer, is equal to or greater than the requirement for growth in muskoxen.

Requirements of N for summer growth of muskoxen and other northern ruminants such as reindeer and caribou (820 mgN/kg$^{0.75}$; McEwan and Whitehead 1970) may be similar to those of more temperate species such as white-tailed deer (*Odocoileus virginianus*; 920 - 1060 mgN/kg$^{0.75}$; Asleson et al. 1996). Winter requirements for N in young muskoxen would be lower than for summer because growth is slow (Fig. 1.2), food intakes are low, and urinary losses of N may be small (Larter and Nagy 2001b). Consequently, young muskoxen may only require N for maintenance at similar levels to cervids such as white-tailed deer (370 - 610 mgN/kg$^{0.75}$; Asleson et al. 1996) and moose (*Alces alces*; 627 mgN/kg$^{0.75}$; Schwartz et al. 1987).

Gains of N by muskoxen in summer could be constrained by the abundance of graminoids that provide the major portion of the diet. Graminoids are low in N (4.7-7.2 % CP; Larter and Nagy 2001b) and of low digestibility (43 %; Adamczewski et al. 1994b). Consequently, the availability of plants with higher N concentrations (10-20 % CP) such as willow (*Salix* sp.; Klein and Bay 1990; Klein and Bay 1994) may complement and supplement the consumption of graminoids (Boyd et al 1996). Forage abundance and diversity may therefore influence survival and recruitment of young muskoxen especially in regions with high population density (Gaillard et al. 1998; Larter and Nagy 2001a).

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Table 1.1 Composition of food offered (% dry matter) to yearling muskoxen.

Parameter	Common Supplement	Medium N Supplement	High N Supplement	H
Dry Matter (% as fed)	92.00	90.52	91.72	82
Neutral Detergent Fiber	24.13	24.88	24.28	56
Acid Detergent Fiber	12.00	13.28	11.69	30
Acid Lignin	1.13	2.56	2.31	2
Nitrogen	2.60	2.05	4.02	1
Crude Protein	16.24	12.81	25.13	9
Crude Fat	2.23	1.37	2.01	1
Ash	6.86	6.69	16.45	5

Fig. 1.1 Body Mass of Yearling Muskoxen Recorded Each Week. Body mass of yearling male (n = 5) and female (n = 4) muskoxen from weaning in October 1999 (139 days old) to March 2001 (669 days old). Sexes were significantly ($P < 0.05$) different from 309 to 669 d.

Fig. 1.2 Growth Rates of Male and Female Muskoxen. Growth rates (kg/d) for male (n = 5) and female (n = 4) muskoxen from early winter 2000 to late winter 2001 plotted against median age (days). Sexes differed at 474 days of age.

Fig. 1.3 Body Composition of Yearling Muskoxen Based on Tritium Dilution. Body mass, water space and fat (kg) determined by tritiated water (n = 7). Measures were not significantly different ($P > 0.05$) between sexes (4 male and 3 female) or diets (3 medium N and 4 high N). Different letters within each measure indicate significant pairwise differences ($P < 0.05$).

Fig. 1.4 Subcutaneous Fat Depths of Yearling Muskoxen by Diet. Fat at the rump measured by ultrasound in autumn 2000 (520 days old), and spring 2001 (669 days old). Significant effect of diet in autumn 2000 (n = 9).

Fig. 1.5 Isotopic Ratios of tissues of Yearling Muskoxen. Isotopic enrichment (ppt) of tissues of muskoxen fed medium N or high N supplements. A. $\delta\ ^{15}N$ enrichment: significant differences between hair, plasma and red blood cells, (n = 7, $P^{\circ} < ^{\circ} 0.001$). Plasma (n= 8) differed significantly between October and March and between diets. Significant effect of diet on erythrocytes in March 2001 (n = 7). B. ^{13}C of tissues and diet. Different letters indicate significant ($P < 0.05$) pairwise differences between tissues. Plasma differs between October and March (n = 8).

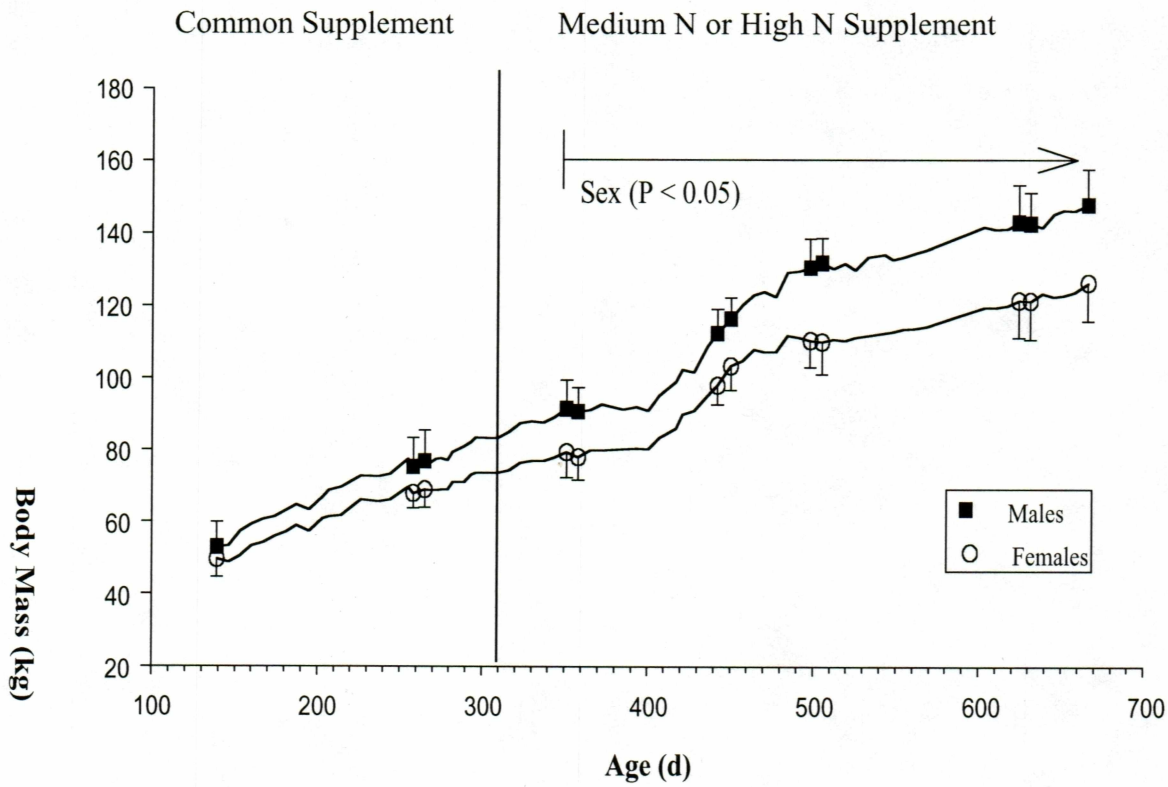

Figure 1.1 — Body Mass of Yearling Muskoxen Recorded Each Week

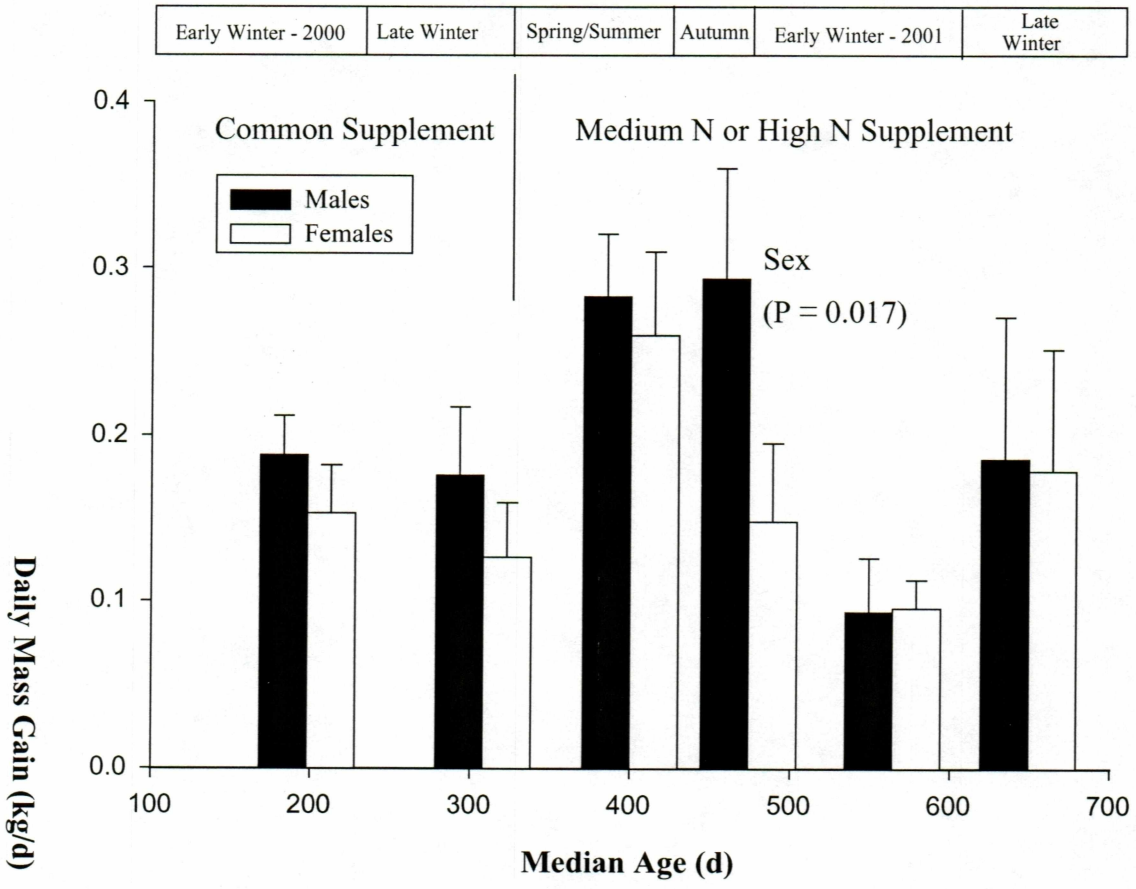

Figure 1.2 — Growth Rates of Male and Female Muskoxen

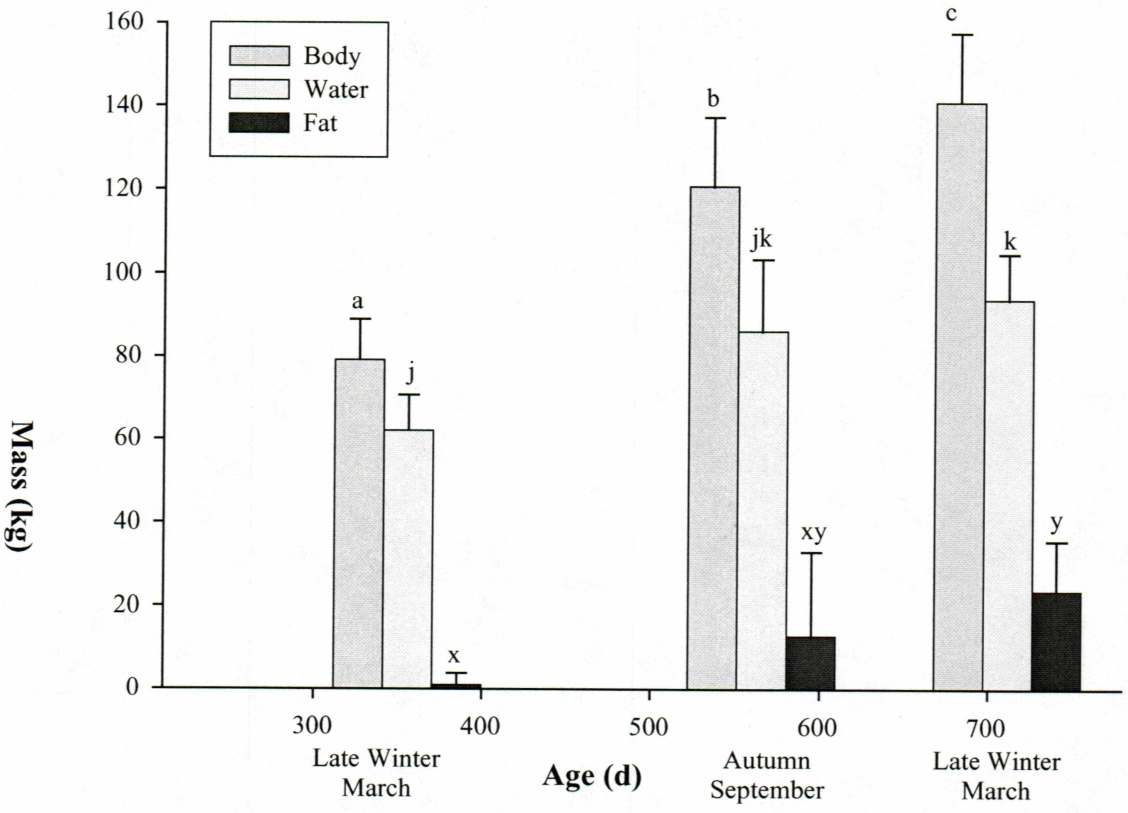

Figure — 1.3 Body Composition of Yearling Muskoxen Based on Tritium Dilution

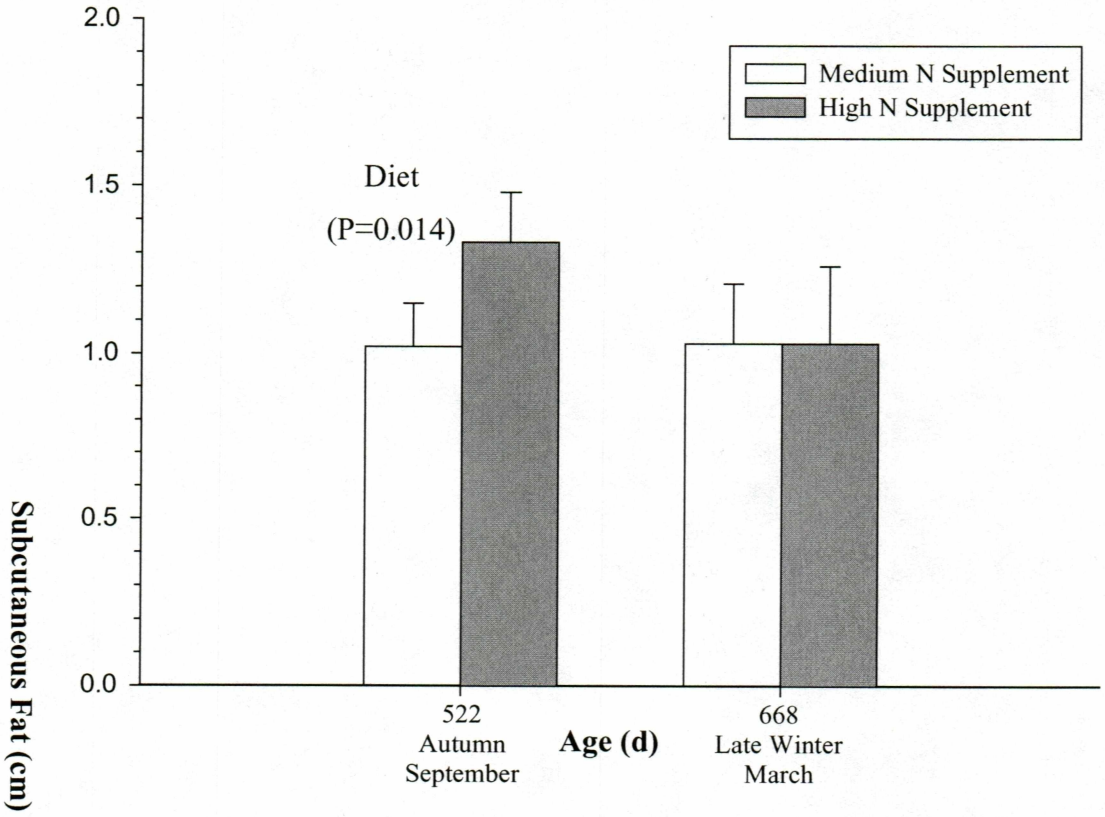

Figure 1.4 -- Subcutaneous Fat Depths of Yearling Muskoxen by Diet

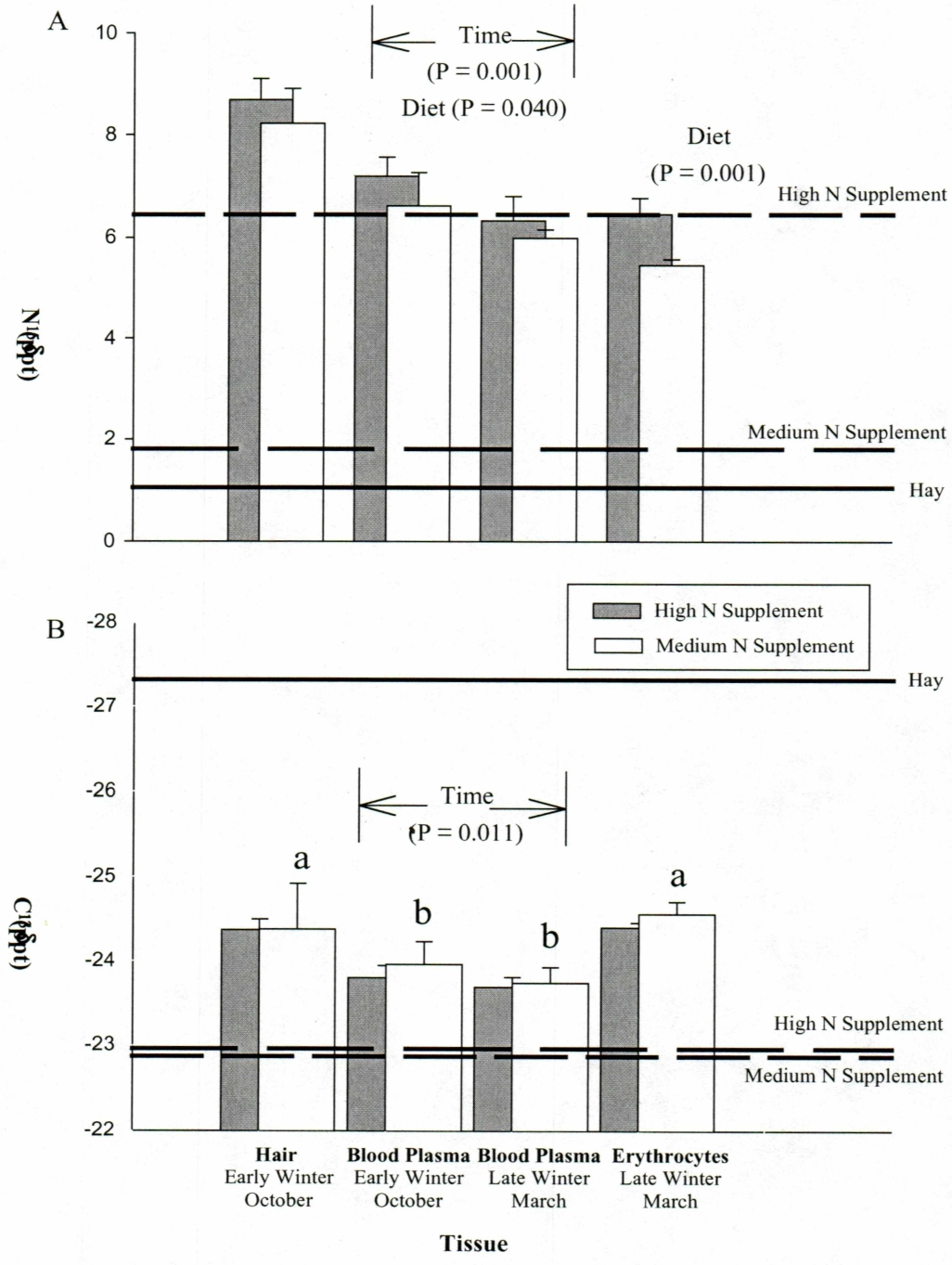

Figure 1.5 -- Isotopic Ratios of Tissues of Yearling Muskoxen

CHAPTER 2

Muskoxen (*Ovibos moschatus*) are the largest grazers in the arctic and subarctic where seasonal changes in light and temperature constrain the growth of plants. Rapid growth of plants in spring (May-June) provides herbivores with high-quality foods that are often low in fiber and high in cell contents (Klein and Bay 1990; Staaland and Olesen 1992). Quality and quantity of foods for herbivores decline from late summer because plants senesce in autumn (Thing et al. 1987; Klein and Bay 1994), and snow may limit access to plants during winter (Forchhammer and Boertman 1993; Ihl and Klein 2001). Muskoxen mainly consume grasses and sedges that are high in fiber and low in both nitrogen (N) and sodium (Na; Forchhammer and Boomsma 1995; Larter and Nagy 1997; Nelleman 1998). Intakes of N may be supplemented by consumption of legumes and dicotyledonous plants (Mulder and Harmsen 1995) while mineral licks can provide a supplemental source of Na in some regions (Thing et al. 1987; Klein and Thing 1989). High densities of muskoxen in small home ranges (H naff and Cr te 1989; Reynolds 1998) may however, limit the diversity and abundance of food (Raillard and Svoboda 2000) and thus exacerbate the seasonal effect on nutrient availability for these large ruminants. Regional differences in growth and production of muskox herds probably reflect the abundance and quality of foods available throughout the year (Olesen et al. 1991; Larter and Nagy 2001)

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Foraging activity of wild muskoxen is low in winter but increases from spring to autumn (Forchhammer 1995; Cote et al. 1997). These activity patterns reflect food intakes that are lowest in winter and highest in summer for both free-living (White et al. 1975; Holleman et al. 1979; Barboza and Bowyer 2001) and captive ruminants at high latitudes (Adamczewski et al. (1994a). High intakes may however, compromise utilization of dietary substrates if digestion and absorption are limited by retention time or capacity of the digestive tract (e.g. Sibly and Calow 1986; Jumars and Martinez del Rio 1999). This trade-off between food intake and digestive efficiency is most likely for grazing ruminants because digestion of fiber requires multiple microbial reactions and prolonged residence in a fermentation region (Alexander 1993; Stevens and Hume 1995).

Retention of dietary energy and nutrients may also vary with season because maintenance and net production of tissues change seasonally. Energy demand for basal metabolism is reduced in winter (Nilssen et al. 1994; Lawler and White 1997) as is the demand of N for hair synthesis (Flood et al. 1989). Thermal costs and fetal development may however, elevate demands for energy and nutrients in winter resulting in mass loss of females (Adamczewski et al. 1997). Metabolic demands for restoration of body mass lost in winter, net growth, and lactation can contribute to utilization of dietary energy and nutrients in summer (Parker et al. 1990; Adamczewski et al. 1994a). High food intakes required to support elevated metabolism in summer may be associated with increases in metabolic turnover and mass of tissues in the digestive tract, liver and kidney (Hammond and Wunder 1991; Hammond et al. 1994) which may consequently alter patterns of digestion, net retention and the cost of maintaining body tissue (Barboza and Bowyer

2000). These effects of growth and reproduction on food intake and retention of energy and nutrients may enhance or diminish the underlying endogenous response to season.

We describe the effects of season and dietary quality on food intake, digestion, metabolism and body composition of captive muskoxen in the subarctic. We used castrated adult males to exclude effects of reproduction and rapid growth on seasonal response. Dietary quality was varied with two mineral supplements of different N content without changing the basal diet of grass hay. Food intake was measured at the start and at the end of the season of plant growth. Efficiency of digesting and absorbing dry matter and its components were measured in spring, summer and winter with lignin as a reference marker. Renal function was assessed in each season by the clearance of inulin whereas retention of energy and N was appraised from repeated measures of water space, lean mass and subcutaneous fat as well as serum and urinary creatinine and urea.

MATERIALS AND METHODS

Muskoxen were held at studied at the R. G. White Large Animal Research Station (Fairbanks, Alaska, USA; 65°N 146°W) under protocol # 00-003 with approval of the Institutional Animal Care and Use Committee, University of Alaska Fairbanks. Seasons at this latitude are described as follows: early winter = October to January, late winter = February to April, spring and summer = May to July, and autumn = August to September. These periods correspond to the annual reproductive cycle of the herd, that is, breeding or rut in autumn, gestation through winter and parturition at the start of spring.

We used 8 non-reproductive adult males (3.8 to 8.8 y) with an average age of 6.0

– 2 y at the end of the study. All animals were excluded from the breeding herd and castrated more than 4 months before the study. Two animals were surgically modified with a ruminal cannula more than four years before the study whereas the remaining six muskoxen were fitted with both ruminal and duodenal cannulae more than 3 months before the start of the study. All animals were healed and maintaining body mass and regular food intake and excretion for 1.5 months before experiments began in May. Animals were housed in individual pens in the spring (May-June) and autumn (August-September), but divided into 2 groups and held in one of 2 large pens (either 0.139 ha or 0.184 ha) during winter (October through March).

Fresh water or snow was provided with grass hay (*Bromus sp.*) ad libitum throughout the year. Pelleted mixtures of grains, roughage and premixes of vitamins and minerals were provided as supplements at 5 gÆkg $^{-0.75}$Æd^{-1} in spring and winter, but increased to 5.7 gÆkg$^{-0.75}$Æd^{-1} during summer. Supplements were produced in a single batch to minimize variation in composition through the study (Alaska Pet and Garden, Anchorage AK). A single consignment of hay was also used within each season to minimize variation in the food offered to muskoxen (Table 2.1). Grass hay was higher in both neutral detergent fiber (NDF) and acid detergent fiber (ADF) than either supplement. Both supplements were higher than hay in the concentration of sulfur (S), calcium (Ca), magnesium (Mg), sodium (Na), copper (Cu) and zinc (Zn; Table 2.1). Sources of N in both supplements included corn, barley and alfalfa whereas fishmeal was included in the high N supplement to provide an additional source of protein that could bypass ruminal fermentation (Van Soest 1994). Crude protein (CP) contents of

dry matter (DM) were lowest in hay (4.5 to 9.6% CP), intermediate for the medium N supplement (11.3% CP) and greatest for the high N supplement (30.0% CP).

Body mass was recorded each week (– 0.5 kg. Tru-Test Model 703 scale; San Antonio, TX) throughout the study. Muskoxen were ranked by size and assigned to one of two groups of similar average mass for each of three study periods: spring (May-June), autumn (August-September) and winter (February-March). Each study period included 2 trials of 4 weeks in a crossover design. Experimental trials consisted of two weeks of acclimation to a supplement followed by one week for measures of food intake and digestion, and a second week for measures of renal function and metabolism from samples of blood and urine. Animals received an equal mix of both supplements at the same daily rate between study periods in spring (trials 1 & 2; May and June), autumn (trials 3 & 4; August and September), and winter (trials 5 & 6; February and March).

Food intake was measured in spring and summer by weighing food bins before and after refilling with fresh hay each morning. Bins were secured to the side of the pen on top of a 2.42˚m^2 wooden platform that facilitated the collection of rejected hay. Subsamples of the supplements were collected each week. Samples of the hay offered, hay rejected, and feces were collected each morning for 5 consecutive days. Samples of rejected hay were not collected during the winter because hay remaining in the feed bins was mixed with fresh hay each day.

Body composition was determined by measures of subcutaneous fat and water space in spring (June), summer (September), and the following winter (March). Subcutaneous fat was measured via ultrasound (– 0.1 cm; Technicare Model #SSD-

210DX, Denver, CO) on the rump at the midpoint of a transect extending from the iliac crest to the ischial tuberosity (Stephenson et al, 1998; Rombach 2000). Water space was measured by dilution of a single intra-jugular dose of tritiated water (^3H_2O) at 1.27 to 1.67˚µCiÆkg^{-1} body mass in 0.9 % NaCl (Sigma Chemicals, St. Louis, MO). All animals were denied access to drinking water, snow or food for 3 h to facilitate equilibration of the dose with body fluids. Blood was sampled from the jugular vein into dry heparinized tubes (Vacutainer Becton Dickinson, Rutherford, NJ) before dosing and at approximately 3, 6 and 24 h from the dose. Plasma was separated at 300-x *g* in a bench centrifuge and stored at —20Œ for analysis.

Animals received an intra-jugular injection of inulin during the fourth week of each experimental trial. Inulin was prepared from equal proportions of chicory root and dahlia tubers (Sigma Chemicals, St. Louis, MO) at 100 g.L^{-1} with 9 g NaCl .L^{-1} in water that was heated to 95¡C to dissolve the inulin and kept warm (30¡C) until dosing. Each animal received 50.9 – 3.3˚g of inulin solution followed by 50 mL of saline (9 g NaCl ·L^{-1}) to ensure full delivery of the dose. Blood was sampled from the jugular vein into evacuated glass tubes (Vacutainer, Becton Dickinson, Rutherford, NJ) before dosing and at approximately 2, 6, and 24 h from the dose. Plasma was separated at 300-x *g* in a bench centrifuge and stored at —20Œ for analysis. Clear plastic sheets attached to wooden frames were placed inside the feeding platforms to collect urine samples after dosing with inulin. Spontaneously voided urine was collected, transferred to plastic bottles, and stored at -20¡ C.

Chemical Analyses & Calculations

Food and fecal samples were combined for each animal, dried at 55¡ C to a constant mass to determine dry matter content, and ground through a # 20 (1.25 mm) screen in a Wiley Mill (A.H. Thomas & Co. Philadelphia, PA) before analysis. Fiber and lignin was analyzed by the methods of Van Soest et al. (1991): NDF was extracted with Na_2SO_3 and lignin was extracted with H_2SO_4 without permanganate. Hemicellulose content was calculated as the difference between NDF and ADF, whereas cellulose content was the difference between ADF and lignin. All values were expressed on a dry matter basis. Gross energy was measured in an adiabatic bomb calorimeter. (Parr Instruments, Boleen, IL). Nitrogen and S were analyzed with an elemental analyzer (CNS2000, LECO Co., St. Joseph, MI). Dietary N was converted to crude protein by assuming that 100g crude protein contained 16g N (Robbins 1993). Ash was determined by combustion in a muffle furnace at 500¡ C and subtracted from DM to measure organic matter. Coefficients of variation for proximate analyses were below 7 %.

Supplements, hay, and feces were digested in a mixture of 70 % v/v HNO_3 (1,000 mL), 32 M H_2SO_4 (200 mL), 70 % v/v $HClO_4$ (343 mL), and water (57 mL) for analysis of minerals. Digestions were performed in sequence from 66¡C to 316¡C over 100 min to provide complete degradation of organic matter. Digests were diluted with distilled, deionized water and assayed by directly coupled plasma spectrometry (Iris DCP, Thermo Elemental, Cheshire, UK).

Consumption of energy, organic components and elements was calculated as the difference between total amount offered and rejected in both hay and supplement. We

assumed that the composition of the supplements offered were the same as that consumed by the animal because little if any of the ration was rejected each day. We also assumed that mineral content of the consumed hay was the same as the hay offered because rejected hay was potentially contaminated by soil and highly variable in mineral concentration. The concentration of each component ingested was calculated as the concentration in total dry mass ingested. We calculated the fraction of dietary components that were apparently removed from the digestive tract by digestion and net absorption as the digestible fraction of the diet. The efficiency of digesting and absorbing each component of the diet was the digestible fraction expressed as a proportion of intake (digestibility). The digestible fraction of each component consumed was calculated from the concentrations of lignin in dry mass consumed and in dry mass defecated (e.g. Barboza and Hume 1992). This calculation assumes that acid lignin is indigestible across all periods. Mature grasses were the primary source of dietary lignin throughout this study, and animals were not exposed to immature forages in which lignin may be most variable (Van Soest 1994). Although acid lignin was less than 5% of dietary DM, the assay was highly reproducible in foods and feces from muskoxen (<10% coefficient of variation) and therefore provides a reliable basis for estimates of digestibility from fibrous foods (Barboza and Jorde 2001).

Blood plasma was assayed for ^{3}H by scintillation counting and corrected for quench and background (Beckman LS6000SE, Beckman Instruments Inc. Redmond WA). Body water kinetics were calculated from the least squares regression of the decline in plasma tritium (ln [H^3]) over time. Coefficients of variation were below 10%

for dosed plasma and below 20% for pre-dose samples. Body water space (W) was calculated from the concentration of ^{3}H in plasma at zero time of the regression (b) as: W (kg) = [Dose (dpm) b (dpm/mL)] x 1000 (mL/kg). Water space was corrected for water in the digestive tract with the assumption that ingesta was 18% body mass with 0.8413g H_2OÆgingestaÅ(Barboza and Blake unpublished data). Net water space (NW) associated with lean tissues was calculated as: NW = [W x 0.9] - [0.8413 x 0.18 x BM]. This calculation assumes that $^{3}H_2O$ space overestimates water space by 10% (Allaye Chan-McLeod et al. 1994; Fancy et al. 1986). Lean mass (NM) was subsequently calculated on the basis of 73.3% water (Adamczewski et al. 1995) as: NM = NW 0.733. Lipid mass (LM) was calculated as the difference between lean and ingesta free mass as: LM = NM — (0.18 x BM). Total protein (TP) was calculated from the relationship described by Adamczewski et al. (1995) as: TP = 0.207 x NM.

Plasma and urine were assayed for urea by the diacetyl-monoxime method (Procedure # 535; Sigma Chemicals, St. Louis MO; Marsh et al. 1965), for creatinine by the alkaline picrate reaction (Procedure # 555, Sigma Chemical; Heineg rd and Tiderstr m, 1973), and for osmolality by vapor pressure (Vapro #5520, Wescor, Logan UT USA). Plasma was deproteinized with trichloroacetic acid for urea analysis and with $ZnSO_4$Æ7H_2O for inulin assays. Inulin was assayed by the reaction of fructose with tryptophan after the method of Waugh (1977). We assumed that inulin was distributed in a single body compartment and excreted at the glomerulus without any other routes of elimination or reabsorption (Levinsky and Lieberthal 1992). Glomerular filtration rate (GFR) was calculated from the clearance of plasma inulin as GFR = kD A; where k is

the linear decline in ln[inulin μgÆml^{-1}] between 2 and 6h from dosing, D is the total dose of inulin, and A is the concentration of inulin in plasma at 2h from dosing. Urinary volume (V) was estimated from GFR and the concentration of creatinine in plasma at 2h from feeding (P) and urine collected after feeding supplements (U) as V = GFR x P U. This calculation assumes that GFR and the concentrations of creatinine do not fluctuate through the period of collection, and that creatinine and inulin are cleared from plasma in a similar fashion (Levinsky and Lieberthal 1992).

We used programs in SYSTAT 10.2 (SPSS Inc. Chicago, IL) to calculate and analyze statistics. Effects of time on repeated measures of body composition, subcutaneous fat, plasma urea, plasma creatinine and plasma osmolality were compared by ANOVA. Measures of intake and digestion were also compared by ANOVA with repeated measures within animals and with dietary supplement (nested within experimental trials) as a factor between animals. Pairwise contrasts were performed with Bonferroni s adjustments for multiple comparisons. Data expressed as proportions or percentages (e.g. digestible fraction and nutrient concentration) were transformed to the arcsine of the square root to meet assumptions of normality for ANOVA (Zar 1974). Paired t-tests were used to compare the composition of hay offered with that rejected by muskoxen. One-sample t-tests were used to compare seasonal digestibilities with zero. Statistical significance was determined as $\alpha > 0.05$. Results are reported as means – one standard deviation (SD).

RESULTS

Body mass declined between April and June in all animals including those that did not undergo surgery in the winter before this study (Figure 2.1). Muskoxen gained mass from 239 – 38 kg to 260 – 37 kg between spring and autumn ($P^{\circ}<^{\circ}0.001$) and maintained body mass to early winter (Figure 2.1). Body mass changes were not associated with changes in water space (159 – 17 kg), lean mass (143 – 17 kg) or protein mass (30 – 4 kg) between spring, autumn and winter ($P > 0.05$; Figure 2.2). Body fat increased from spring (53 – 30 kg) to winter at an average daily rate of 108 – 73 $g.d^{-1}$. Increases in body fat between autumn (68 – 24 kg) and winter (84 – 26; $P = 0.010$; Figure 2.2) were not however, associated with changes in subcutaneous fat which was similar in depth at the rump between autumn (2.1 – 1.2 cm) and winter (2.5 – 1.2 cm; $P = 0.215$).

Muskoxen rejected hay that was lower in N (1.08 – 0.35% vs. 1.19 – 0.33%; $P <0.001$) and higher in lignin (3.59 – 0.79% vs. 2.99 – 0.26%; $P <0.001$) than the hay offered in both spring and autumn. Organic composition of the diet consumed by muskoxen reflected the composition of hay, which was slightly lower in cellulose during autumn than during spring (Table 2.1 and 2.2). Daily intake of DM increased by 74 % from spring to autumn ($P < 0.001$; Table 2.2) with concomitant increases in intakes of organic matter and gross energy. Increases in the intake of fiber were associated with increased consumption of lignin from spring (0.067 – 0.018 $^{\circ}kg.d^{-1}$) to autumn (0.109 – 0.038 $kg.d^{-1}$). Digestibilities of organic matter, gross energy and fiber were not affected by supplement ($P > 0.05$) or by changes in intake between spring and autumn (Table 2.2).

Hay was the principal source of ingested dry matter (97 %), organic matter (92 %), gross energy (92 %), cellulose (97 %), hemicellulose (100 %), and lignin (93%) during spring and autumn. Lignin in hay and feces were therefore used to estimate digestive efficiency for organic components of the diet during winter. Digestibility of dry matter declined to 50.1 – 6.7°% in winter ($P < 0.001$). Digestibilities were also lower in winter than in spring or autumn for organic matter (55.1 – 6.5 %; $P = 0.020$), gross energy (46.2 – 8.5 %; $P < 0.001$), cellulose (64.9 – 4.8 %; $P = 0.004$) and hemicellulose (53.2 – 7.3 %; $P < 0.001$).

Hay was the principal source of dietary Ca (92%), Mg (87%) and K (94%) in both spring and autumn. Dietary concentrations and daily intakes of these elements mainly reflected changes in the intake of hay (Tables 2.1 and 2.3). High intakes of hay in autumn did not affect the low digestive efficiency for Ca and Mg, whereas the high digestibility of K was reduced in autumn compared with spring (Table 2.3). Digestive efficiency of Na was also high, but unlike K, supplements were the principal of source of Na (78%) for muskoxen. Dietary Cu and Zn were poorly digested in both spring and autumn even though supplements provided 30% of ingested Cu and 36% of ingested Zn (Table 2.3). Digestible intakes of Ca, Mg, Cu and Zn were highly variable and similar between spring and autumn even though digestible intakes of all other dietary components increased with absolute intakes between spring and autumn (Table 2.4). These digestive balances for Cu and Zn were not significantly different from zero whereas those for Ca and Mg were low but positive (Table 2.4).

Supplements provided 30 to 40% of ingested S, and 20 to 30% of ingested N

during spring but high intakes of hay provided 78 to 84% of S and 83 to 90% of N consumed in autumn. Increases in dietary concentration of S and N between spring and autumn (Table 2.3) were mainly due to increases in the content of N and S in hay (Table 2.1). Digestive efficiency for N was similar between supplements and between seasons even though N intake more than doubled on medium N (31.4 – 6.79 vs. 74.5 – 12.3 $g.d^{-1}$) and high N (37.3 – 7.98 vs. 87.0 – 21.7) supplements between spring and autumn respectively.

Consumption of N from both medium and high N supplements increased plasma urea concentration in a similar manner during spring and winter but not during autumn when intakes of hay were high (Table 2.5). Plasma urea was highest in winter and remained at similar levels between 2 and 6 hours from feeding supplements. Creatinine concentrations were also stable between 2 and 6 hours from feeding in winter when plasma concentrations were lower than either autumn or spring. Solute concentration of plasma and urine were not affected by season or supplemental feeding (Tables 2.5 and 2.6). Consumption of high N supplement did however, increase urinary concentrations of urea and creatinine in spring but did not affect urinary composition in autumn (Table 2.6).

Glomerular filtration rates were similar between supplements but lowest in spring and similar between autumn and winter (Figure 2.3). Fractional clearance (k) of inulin was variable and similar among periods (-0.267 – 0.153 h^{-1}) as was the dilution space for inulin (D A; 117 – 53 kg). The mass ratio of plasma creatinine to urinary creatinine was similar between spring (0.015 – 0.009) and autumn (0.018 – 0.004) and therefore

estimated urinary outflow was commensurate with GFR which was also greater in autumn than in spring (Figure 2.3).

DISCUSSION

Mass changes in muskoxen are modulated by season even when food is available ad libitum. Loss of mass through late winter and spring in nonreproductive males (Figure 2.1) probably reflects an endogenous pattern similar to other northern ungulates such as moose (Schwartz et al. 1987a). Mass gains in summer may partly reflect rates of mass loss in the previous winter, that is, high rates of loss may be followed by large gains before the following winter (Renecker and Samuel 1991; Parker et al. 1993). This suggestion is consistent with mass gains that vary annually, for example, nonreproductive muskoxen gained 17 – 5% of minimal body mass during this study (Figure 2.1) but only 8 – 5% of minimal body mass in the following year (2001). Net gains of mass in young muskoxen and reproductive females are also greatest in summer and autumn (White et al. 1989; Adamczewski et al. 1992; Peltier and Barboza unpublished data). It is likely that these mass gains are ultimately controlled by photoperiod but mediated by various endocrine secretions such as thyroid hormones (Ryg 1983; Nilssen et al. 1994), growth hormone, (Ryg and Langvatn 1982), insulin-like growth factor (Adamczewski et al. 1992) and gonadal steroids (Leader-Williams and Ricketts 1981; Argo et al. 1999; Gedir and Hudson 2000).

Mass gained by muskoxen was mainly associated with fat (Figure 2.2). Fat was probably deposited between muscles and among viscera (Adamczewski et al 1995) because depths of subcutaneous fat were similar between autumn and winter even though

body fat was gained during this period (Figure 2.2). Subcutaneous depots may be conserved more than other depots in muskoxen since fat depths are also maintained through winter pregnancy in captive females (Rombach 2000). Conservation of back fat may however reflect the large deposition of fat in captive animals compared with wild muskoxen. Fat content on the basis of ingesta free mass was 26 – 12% in June and 38 – 9% in March for nonreproductive males whereas young nonreproductive females were only 12% and 23% body fat in April and November on Victoria Island (Adamczewski et al.1997).

Accumulation of energy as body fat from spring to winter was supported by high intakes of digestible energy during autumn (Table 2). Energy gained as body fat between spring and winter was equivalent to 65 – 38 $kJ.kg^{-0.75}.d^{-1}$ based on the assumption that depot fat contains 39.3 $kJ.g^{-1}$ (Blaxter 1989). Fat deposition is equivalent to 143 – 88 $kJ.kg^{-0.75}.d^{-1}$ of digestible energy if assimilated energy is converted to tissue with an efficiency of 67.5% (Barboza and Bowyer 2001). Digestible energy intake corrected for energy retained as tissue is the maintenance energy requirement for the animal, which was 826 – 255 $kJ.kg^{-0.75}.d^{-1}$. This estimate is 1.8 times the fasted energy expenditure of muskoxen measured from June to August (Lawler and White 1997) and reflects the added costs of mobility and thermoregulation (Fancy and White 1985). Maintenance requirements for energy probably follow the same seasonal pattern as fasting metabolic rate, which is 33% lower in winter than in spring (Lawler and White 1997). This suggestion is supported by the low digestible energy intake in spring (554 $kJ.kg^{-0.75}.d^{-1}$; Table 2.4) which was 33% lower than the maintenance estimate for autumn but does not

include any additional energy returned from tissue mobilization.

Fiber digestion provided most of the energy assimilated by muskoxen. Digestible intakes of cell walls were equivalent to 316 – 69 $kJ.kg^{-0.75}.d^{-1}$ in spring and 529 – 137 $kJ.kg^{-0.75}.d^{-1}$ in autumn for cellulose (17.49 $kJ.g^{-1}$) and hemicellulose (17.49 $kJ.g^{-1}$ xylans; Blaxter 1989). These estimates are 57 – 5% of digestible energy ingested in both spring and autumn even though intakes of cellulose and hemicellulose were 58 to 77% greater in autumn than in spring (Tables 2.2 and 2.4). Consistent efficiency of fiber digestion (Table 2.2) indicates that fermentative systems were maintained in proportion to substrate load, that is, cellulolytic efficiency did not diminish with intake. Consistent digestive efficiencies between seasons suggest changes in gut microflora, digestive morphology, gut capacity and digesta passage. Microbial species in muskoxen include cellulolytic and xylanolytic bacteria common to other arctic ungulates (Dehority 1984). Although ruminal populations of microbes increase from winter to spring in wild reindeer (*Rangifer tarandus*; Orpin et al. 1985) the number and diversity of microbes may reflect seasonal changes in the diet (Dehority 1984). Increases during summer in the mass of rumen tissue of nonreproductive female (Adamczewski et al 1997) may be associated with increases in ruminal surface area (Hoffmann and Nygren 1992; Soveri and Nieminen 1995) but these changes may also reflect seasonal shifts in the diet. Unfortunately growth or reproduction may also confound seasonal response to a constant diet in muskoxen. Growing muskoxen increase dry matter intake (38 to 108 $g.kg^{-0.75}.d^{-1}$), passage rate and digesta fill during summer with a small loss in digestive efficiency (81% to 74% DM; Holleman et al. 1984; White et al. 1987), whereas adult female muskoxen fed hay and pelleted supplement also

lose digestive efficiency in summer (71 to 56% DM) when dry matter intake (39 to 45 $g.kg^{-0.75}.d^{-1}$) and passage rate increase without a change in digesta fill (Adamczewski et al. 1994). Low digestibility of fiber during winter in nonreproductive males from this study are similar to those measured for adult males and females on a similar diet by Adamczewski et al. (1994b). These data suggest a decline in fermentative activity during winter which will be examined in a subsequent report on measures of digesta kinetics and fermentative responses to standard dietary substrates across seasons in nonreproductive male muskoxen.

Digestive efficiency for compounds containing N and S were also unchanged by intake, which increased by over 130% between autumn and spring (Table 2.3). Conservation of lean mass and body protein between spring and winter suggests that digestible intakes of hay with supplement were adequate for maintenance of body protein (Figure 2.2) and for seasonal growth of hair. This suggestion is supported by similar growth of hair and lean mass between groups of young muskoxen fed either medium N or high N supplements with hay (Peltier and Barboza unpublished data). Annual growth of underwool deposits approximately 2.3 kg in adult muskoxen over 152 days between spring (1 May) and the end of autumn (30 September; Flood et al 1989). Net synthesis of hair is therefore equivalent to 39.3 – 4.6 $mgN.kg^{-0.75}.d^{-1}$ and 11.4 – 1.3 $mgS.kg^{-0.75}.d^{-1}$ for hair containing 16.04 % N and 2.92 % S (Peltier and Barboza unpublished data). Digestible intakes from hay with the medium N supplement were 296 to 731 $mgN.kg^{-0.75}.d^{-1}$ and 5 to 35 $mgS.kg^{-0.75}.d^{-1}$ for spring and autumn respectively when corrected for hair deposition (Table 2.4). Digestible intakes of N for muskoxen in spring

are similar to estimates of digestible N required for winter maintenance of moose (254 $mgN.kg^{-0.75}.d^{-1}$; Schwartz et al. 1987b) and white-tailed deer (320 $mgN.kg^{-0.75}.d^{-1}$: Asleson et al. 1996). High digestible intakes of N by muskoxen in autumn are similar to those required for maintenance of growing caribou (462 $mgN.kg^{-0.75}.d^{-1}$; *Rangifer tarandus* McEwan and Whitehead 1970) and white-tailed deer (610 to 920 $mgN.kg^{-0.75}.d^{-1}$; *Odocoileus virginianus*; Asleson et al. 1996). Dietary concentrations of 12.5 $gN.kg^{-1}$ and 1.0 $gS.kg^{-1}$ may therefore meet or exceed requirements for maintenance of adult muskoxen even when intakes are low from winter through spring. High intakes of DM in summer and autumn may however, sustain absolute intakes of N and S when dietary concentrations are low (Tables 2.2 and 2.3; Barboza and Bowyer 2001; Schwartz et al. 1987b).

Dietary N supplies probably exceeded requirements of nonreproductive muskoxen during spring and winter because dietary protein was apparently catabolized to urea circulating in plasma within 2 hours of feeding both supplements (Table 2.5). An increase in urinary urea following feeding of high N compared with medium N supplement (Table 2.6) is consistent with an excess of dietary N, and with catabolism of dietary protein in the digestive tract or in the liver (Annison and Bryden 1998). Small increments in plasma creatinine after feeding in spring probably reflect changes in renal clearance of creatinine. The maintenance of plasma osmolality between feeding times and seasons (Table 2.5) suggests that intakes of solutes including urea and electrolytes probably elevate GFR after feeding in spring and winter whereas large and frequent consumption of hay through the day in autumn probably maintain solute loads and thus GFR at high levels through

autumn (Figure 2.3). GFR of nonreproductive males in autumn was 0.13 $mL.kg^{-1}.min^{-1}$ which is lower than that reported for clearance of inulin in two adult female muskoxen during June (0.75-0.93 $mL.kg^{-1}.min^{-1}$; Tedesco et al. 1993). Differences in renal function may reflect differences in temperature, diet, and water availability between the studies (Li et al. 2000) as well as food intake and reproductive state of the animals. Similarly, seasonal changes in renal and hepatic function may underlie changes in plasma urea and creatinine of nonreproductive males (Table 2.5) as suggested for wild muskoxen (Larter and Nagy 2001b) but this suggestion awaits confirmation from seasonal measures of urea kinetics in muskoxen.

Increased urinary excretion between spring and summer (Figure 2.3) was probably associated with greater digestible intakes (Table 2.4) and elimination of solutes such as K and Na. High dietary concentrations of K can however, affect the retention of Na, Mg and Ca (Barboza 1995; Groff and Gropper 1999). Although high intakes of K are common among northern herbivores (Staaland et al 1980), excess K can increase urinary and fecal losses of water as well as the urinary loss of Na (Staaland et al. 1998). A reduction in digestive efficiency for K in muskoxen between spring and autumn may be associated with greater losses of water in feces during autumn (Table 2.3). Average digestible intakes of sodium in muskoxen (7.64 to 9.58 $mg.kg^{-1}.d^{-1}$) exceeded the requirement for maintenance of white-tailed deer (3.27 $mg.kg^{-1}.d^{-1}$; Hellgren and Pitts 1997) and therefore probably did not constrain digestion or metabolism (Staaland and Garmo 1987; Robbins 1993). Most of the ingested Na was derived from supplements, whereas hay provided only 21.52% of ingested Na at just 1.85 $mg.kg^{-1}.d^{-1}$. Consumption

of graminoid plants that are low in Na may therefore limit digestion and metabolism of muskoxen in both summer (Staaland and Thing 1991) and winter (Forchammer and Boomsma 1995) unless supplementary sources of Na are available in soils (Klein and Thing 1989) or other vegetation (Staaland and S b¿ 1993).

Low demands and accumulation of minerals in bone and liver probably minimize digestive uptakes of Ca, Mg, Cu and Zn in nonreproductive muskoxen fed supplements through the year (Table 2.4). Although small amounts of dietary Ca and Mg are associated with absorption from the digestive tract (Wadhwa and Care 2000) and with acid-base balance (Campbell and Hewitt 2000) homeostasis is achieved by controlling uptake in relation to net changes in bone (Robbins 1993; Groff and Gropper 1999). Seasonal changes in bone density of mature muskoxen are probably much smaller than those of deer producing antlers (Grasman and Hellgren 1993; Baxter et al. 1999; Heinrich et al. 1999) because digestible intakes of Ca were only $5mg,kg^{-1}.d^{-1}$ in muskoxen whereas 32-46 $mgCa,kg^{-1}.d^{-1}$ is absorbed from the diet by red deer (*Cervus elaphus*) during antler growth (Muir et al. 1987). Digestive uptakes of Cu and Zn that were near zero for muskoxen probably reflect high hepatic reserves of these elements (Barboza and Blake 2001) because liver concentrations in this captive population are greater than those of wild muskoxen and exceed levels that are considered adequate for domestic cattle (Barboza et al. unpublished data). Dietary levels below 5 mg $Cu.kg^{-1}$ DM and 15 mg $Zn.kg^{-1}$ DM are considered low for domestic ruminants (National Research Council 2000; 2001). The apparent adequacy of these low dietary levels is in part a reflection of the high intakes of DM and the low productive demands of nonreproductive males. Demands for

Cu, Zn, Ca and Mg in lactating females and growing muskoxen are probably higher and may be assessed by factorial increments on intakes for nonreproductive males. Seasonal food intake may be limited by changes in digestion and metabolic demand of muskoxen. Increases in ruminal, kidney and liver tissue of female muskoxen from Victoria Island (Adamczewski et al. 1997) suggests an increase in the capacity to digest, absorb and metabolize energy and nutrients in summer. Although these morphological changes may be stimulated by diet (Jiang and Hudson 1996) they may also underlie increments in metabolic rate measured in captive animals (Nilssen et al. 1994; Lawler and White 1997). Maximum intakes of nonreproductive males during summer and autumn are probably not constrained by digestive and absorptive efficiency (Table 2.2 and 2.3) but by the capacity to avoid toxic accumulations of metabolites within the digestive tract (e.g. unabsorbed acids from fermentation) or within circulation (e.g. K; Illius and Jessop 1996). Deposition of fat and protein in tissues would provide a sink for absorbed products which favors continued food intake as long as digestion and absorption are not constrained (e.g. Hammond et al. 1994). Selection and consumption of plants that provide complimentary intakes of nutrients with energy probably rests on a combination of allometry, physiological feedbacks and learned responses (Day et al 1998; Provenza et al. 1998; Barboza and Bowyer 2000). For example, captive muskoxen maximize nutrient intakes by selecting leaves that are high in N and low in lignin from hay, whereas wild muskoxen select different proportions of forbs and graminoid plants to meet varying demands for maintenance growth and lactation in summer (Forchhammer and Boomsma 1995). Muskoxen combine plasticity of digestive and metabolic systems with body

composition to efficiently load nutrients and energy in the brief arctic summer (sensu Barboza and Jorde 2001; 2002). These physiological patterns ultimately affect habitat use and population dynamics (Illius and Gordon 1999) of these large herbivores in their small home ranges.

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Table 2.1 Feed composition for adult muskoxen. Dry matter composition of grass hay and supplements offered to nonreproductive male muskoxen from May 2000 to March 2001 (mean ± SD).

Component	Medium N Supplement	High N Supplement	Spring Grass Hay	Autumn Grass Hay	W Gra
Dry Matter ($g.100g^{-1}$ as fed)	91.3 ± 1.8	92.3 ± 1.4	88.0 ± 1.6	82.3 ± 1.1	
Gross Energy ($kJ.g^{-1}$)	17.0 ± 0.1	16.0 ± 0.1	17.8 ± 0.3	18.1 ± 0.4	
Organic Matter ($g.100g^{-1}$)	92.3 ± 0.6	83.3 ± 1.3	92.3 ± 0.3	93.2 ± 1.0	
NDF ($g.100g^{-1}$)	24.1 ± 0.5	24.0 ± 0.3	62.1 ± 0.5	59.8 ± 4.7	
Hemicellulose ($g.100g^{-1}$)	11.4 – 0.9	12.7 – 0.3	28.0 – 0.2	28.0 – 2.3	
ADF ($g.100g^{-1}$)	12.6 ± 0.7	11.3 ± 0.4	34.1 ± 0.2	31.8 ± 2.4	
Cellulose ($g.100g^{-1}$)	10.2 – 0.2	9.8 – 0.3	30.9 – 0.1	29.0 – 1.5	
Acid Lignin ($g.100g^{-1}$)	2.5 ± 2.0	1.5 ± 0.1	3.2 ± 0.1	2.7 ± 0.3	
Nitrogen ($g.100g^{-1}$)	2.12 ± 0.06	4.08 ± 0.10	0.94 ± 0.1	1.53 ± 0.3	
Sulfur ($g.kg^{-1}$)	3.02 – 0.14	4.28 – 0.11	0.61 – 0.2	1.19 – 0.2	
Calcium ($g.kg^{-1}$)	3.17 – 0.45	2.31 – 0.54	3.22 – 0.7	3.25 – 0.5	
Magnesium ($g.kg^{-1}$)	1.36 – 0.09	1.28 – 0.13	0.82 – 0.1	0.88 – 0.1	
Potassium ($g.kg^{-1}$)	7.64 – 2.85	7.33 – 2.73	11.6 – 1.2	10.7 – 0.3	
Sodium ($g.kg^{-1}$)	6.89 – 0.87	6.29 – 1.57	0.18 – 0.1	0.14 – 0.1	
Copper ($mg.kg^{-1}$)	15.14 – 1.49	14.06 – 0.84	2.45 – 0.1	3.98 – 0.1	
Zinc ($mg.kg^{-1}$)	51.80 – 2.85	58.49 – 9.71	8.53 – 0.2	10.6 – 0.3	

Table 2.2 — Composition, intake and digestibility. Organic composition of ingested diet (gÆgDM^{-1} or kJ.gDM^{-1}), daily intake (kg or MJ), and digestive efficiency (digestibility; %) of grass hay and supplements in nonreproductive male muskoxen (n = 8) during spring (May-June; 239 – 39 kg body mass) and autumn (August-September; 260 – 37 kg body mass).

	Composition (g.100g^{-1}DM)		Daily Intake (kg)		Digestibility (%)	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
Dry Matter	-	-	2.75^{a} ± 0.54	4.75^{b} ± 0.74	69.1 ± 8.56	71.1 ± 8.4
Gross Energy*	17.7^{a} – 0.2	18.0^{b} – 0.3	48.6^{a} ± 9.2	85.6^{b} ± 13.8	69.0 ± 8.85	68.7 ± 9.0
Organic Matter	92.5 – 1.5	92.3 – 1.4	2.55^{a} ± 0.52	4.39^{b} ± 0.71	73.7 ± 7.38	73.1 ± 7.9
NDF	58.1 – 1.0	56.0 – 5.7	1.60^{a} ± 0.30	2.67^{b} ± 0.60	67.8 ± 9.24	72.2 ± 7.5
Hemicellulose	26.0 – 1.9	26.8 – 2.5	0.72^{a} ± 0.16	1.28^{b} ± 0.26	69.8 ± 11.3	73.3 ± 8.0
ADF	32.2^{a} – 2.1	29.2^{b} – 3.5	0.88^{a} ± 0.15	1.39^{b} ± 0.30	66.1 ± 8.36	68.7 ± 6.6
Cellulose	29.6^{a} – 1.6	26.9^{b} – 2.9	0.81^{a} ± 0.14	1.28^{b} ± 0.27	71.5 ± 7.81	75.8 ± 6.4

ab different superscripts indicate significant differences between seasons ($P < 0.05$).

* Composition (kJ.g^{-1}), daily intake (MJ).

Table 2.3 Minerals. Elemental composition of ingested diet (gÆkg^{-1} or mg.kg^{-1}DM), daily intake (g or mg), and digestive efficiency (digestibility; %) of grass hay and supplement in nonreproductive male muskoxen (n = 8) during spring (May-June; 239 – 39 kg body mass) and autumn (August-September; 260 – 37 kg body mass).

	Composition (g.kg^{-1}DM)		Daily Intake (g)		Digestibility	
	Spring	Autumn	Spring	Autumn	Spring	
Nitrogen	12.53^{a} – 1.63	16.91^{b} – 2.14	34.4^{a} – 7.8	80.7^{b} – 18.2	61.1 – 10.9	(
Sulfur	0.99^{a} – 0.08	1.37^{b} – 0.12	2.73^{a} – 0.57	6.53^{b} – 1.29	29.8 – 21.6	4
Calcium	3.19 – 0.57	3.19 – 0.46	8.95^{a} – 2.98	15.0^{b} – 2.55	27.5 – 25.6	1
Magnesium	0.87^{a} – 0.03	0.9^{b} – 0.05	2.41^{a} – 0.52	4.30^{b} – 0.59	18.6 – 24.1	
Potassium	11.05^{a} – 1.00	10.47^{b} – 0.29	30.7^{a} – 8.02	49.7^{b} – 7.48	93.5^{a} – 4.4	
Sodium	0.77 – 0.25	0.62 – 0.14	2.04^{a} – 0.48	2.86^{b} – 0.36	88.6 – 9.98	8
Copper *	3.78^{a} – 0.35	4.78^{b} – 0.19	10.3^{a} – 1.8	22.6^{b} – 3.0	16.5 – 31.6	(
Zinc*	13.17^{a} – 0.76	14.08^{b} – 0.88	35.9^{a} – 5.7	66.7^{b} – 10.3	-20.7 – 43.7	(

ab different superscripts indicate significant differences between seasons ($P < 0.05$).

* composition (mg.kg^{-1}), daily intake (mg).

Table 2.4 Intake per metabolic body weight. Daily intake of digestible energy, plant fiber and elements by nonreproductive male muskoxen (n = 8) during spring (May-June; 239 – 39 kg body mass) and autumn (August-September; 260 – 37 kg body mass).

Component	Spring	Autumn
Dry Matter ($g.kg^{-0.75}.d^{-1}$)	$31.4^{a} \pm 6.8$	$53.0^{b} \pm 13.5$
Gross Energy ($kJ.\ kg^{-0.75}.d^{-1}$)	$554^{a} \pm 117$	$923^{b} \pm 242$
Cellulose ($g.kg^{-0.75}.d^{-1}$)	$9.54^{a} \pm 1.71$	$15.22^{b} \pm 3.85$
Hemicellulose ($g.kg^{-0.75}.d^{-1}$)	$8.34^{a} \pm 2.38$	$14.75^{b} \pm 4.02$
Nitrogen ($mg.kg^{-0.75}.d^{-1}$)	$336^{a} \pm 131$	$768^{b} \pm 252$
Sulfur ($mg.kg^{-0.75}.d^{-1}$)	$15.9^{a} - 11.2$	$46.6^{b} - 19.7$
Calcium ($mg.kg^{-0.75}.d^{-1}$)	$43.9_{x} - 41.7$	$78.6_{x} - 87.7$
Magnesium ($mg.kg^{-0.75}.d^{-1}$)	$7.1_{x} - 9.7$	$17.5_{x} - 21.7$
Potassium ($mg.kg^{-0.75}.d^{-1}$)	$470^{a} - 137$	$655^{b} - 151$
Sodium ($mg.kg^{-0.75}.d^{-1}$)	$30.0^{a} - 7.4$	$38.3^{b} - 6.1$
Copper (_$g.kg^{-0.75}.d^{-1}$)	$29.4_{y} - 54.5$	$19.8_{y} - 144.2$
Zinc (_$g.kg^{-0.75}.d^{-1}$)	$-117_{y} - 249$	$-3_{y} - 387$

ab different superscripts indicate significant differences between seasons ($P < 0.01$).

x subscript indicates that mean is significantly different from zero ($P < 0.05$).

y subscript indicates that mean is not significantly different from zero ($P > 0.05$).

Table 2.5 Plasma urea, creatinine, and solutes. Plasma concentrations of urea ($\mu g.mL^{-1}$), creatinine ($\mu g.mL^{-1}$), and solutes ($mOsmol.kg^{-1}$) before feeding supplement (pre-feeding) and 3 h after feeding supplement (post-feeding) to muskoxen (n = 8) during spring (May and June), autumn (August and September) and winter (February and March).

Plasma Metabolite	Supplement Feeding	Spring	Autumn	Winter
Urea (µgÆmL)	Pre-feeding	$127.6^{a}_{x} - 33.8$	$117.6^{a} - 31.5$	$163.2^{b}_{x} - 35.1$
	Post-feeding	$137.3^{a}_{y} - 28.0$	$120.1^{a} - 35.6$	$179.8^{b}_{y} - 39.0$
Creatinine (µgÆmL)	Pre-feeding	$13.8^{a}_{x} - 2.9$	$13.6^{a} - 2.1$	$8.7^{b} - 2.1$
	Post-feeding	$15.6^{a}_{y} - 2.6$	$13.9^{b} - 2.2$	$10.1^{b} - 3.3$
Osmolality ($mOsmolÆkg^{-1}$)	Pre-feeding	271.2 – 12.4	271.9 – 10.1	271.7 – 22.4
	Post-feeding	273.9 – 11.1	267.7 – 8.1	258.6 – 35.0

ab different superscripts indicate significant differences between seasons ($P < 0.05$).

xy different subscripts indicate significant differences between levels before and after feeding supplement ($P < 0.05$).

Table 2.6 Urinary urea, creatinine, and solutes. Urinary concentrations of urea ($\mu g.mL^{-1}$), creatinine ($\mu g.mL^{-1}$), and solutes ($mOsmol.kg^{-1}$) after feeding supplements with medium N or high N to muskoxen during spring (May and June), and autumn (August and September).

	Spring		Autumn	
Urinary Metabolite	Medium N Supplement	High N Supplement	Medium N Supplement	High N Supplement
Urea ($\mu g.mL^{-1}$)	$2426_x - 1174^7$	$4283_y - 1861^8$	$4890_y - 482^6$	$4433_y - 1339^7$
Creatinine ($\mu g.mL^{-1}$)	$1194_x - 474^7$	$1615_y - 1020^8$	$1019_{xy} - 575^6$	$823_{xy} - 314^7$
Osmolality ($mOsmol.kg^{-1}$)	$757 - 144^7$	$774 - 254^7$	$806 - 169^5$	$859 - 97^6$

xy different subscripts indicate significant differences between groups ($P < 0.05$).

5-8 superscripts indicate samples size (n).

Figure 2.1 -- Weekly Body Mass of Eight Adult Muskoxen. Lines indicate individual records (A). Solid circles mark records of two animals cannulated more than four years prior to the study whereas all other animals were cannulated over 3 months from the start of the study. Different letters indicate significant differences ($P < 0.001$) between study periods during spring (May and June), autumn (August and September) and winter (February and March). Patterns of body mass are expressed as a ratio to the minimum mass for each individual (B) Different letters indicate significant differences ($P < 0.001$) in absolute body mass between 14 April, 25 June and 15 December (mean – SD).

Figure 2.2 -- Body Composition of Adult Muskoxen Based on Tritium Dilution. Mass (kg) of water, lean tissue, fat and protein (A) in nonreproductive male muskoxen ($n = 8$) during spring (June), autumn (September) and winter (March). Different letters indicate significant differences between seasons ($P < 0.05$; mean – SD).

Figure 2.3 —Glomerular Filtration Rate and Urinary Volume of Adult Muskoxen. Glomerular filtration rate (GFR; inulin clearance; $L.h^{-1}$) in nonreproductive male muskoxen during spring (June; $n = 16$), autumn (September; $n = 15$) and winter (March; $n = 14$). Urinary excretion rate ($mL.d^{-1}$) was derived from GFR, and the mass ratio of plasma to urine for creatinine during spring ($n=15$) and autumn ($n=10$). Different letters indicate significant differences for each measure between seasons ($P < 0.05$; mean – SD).

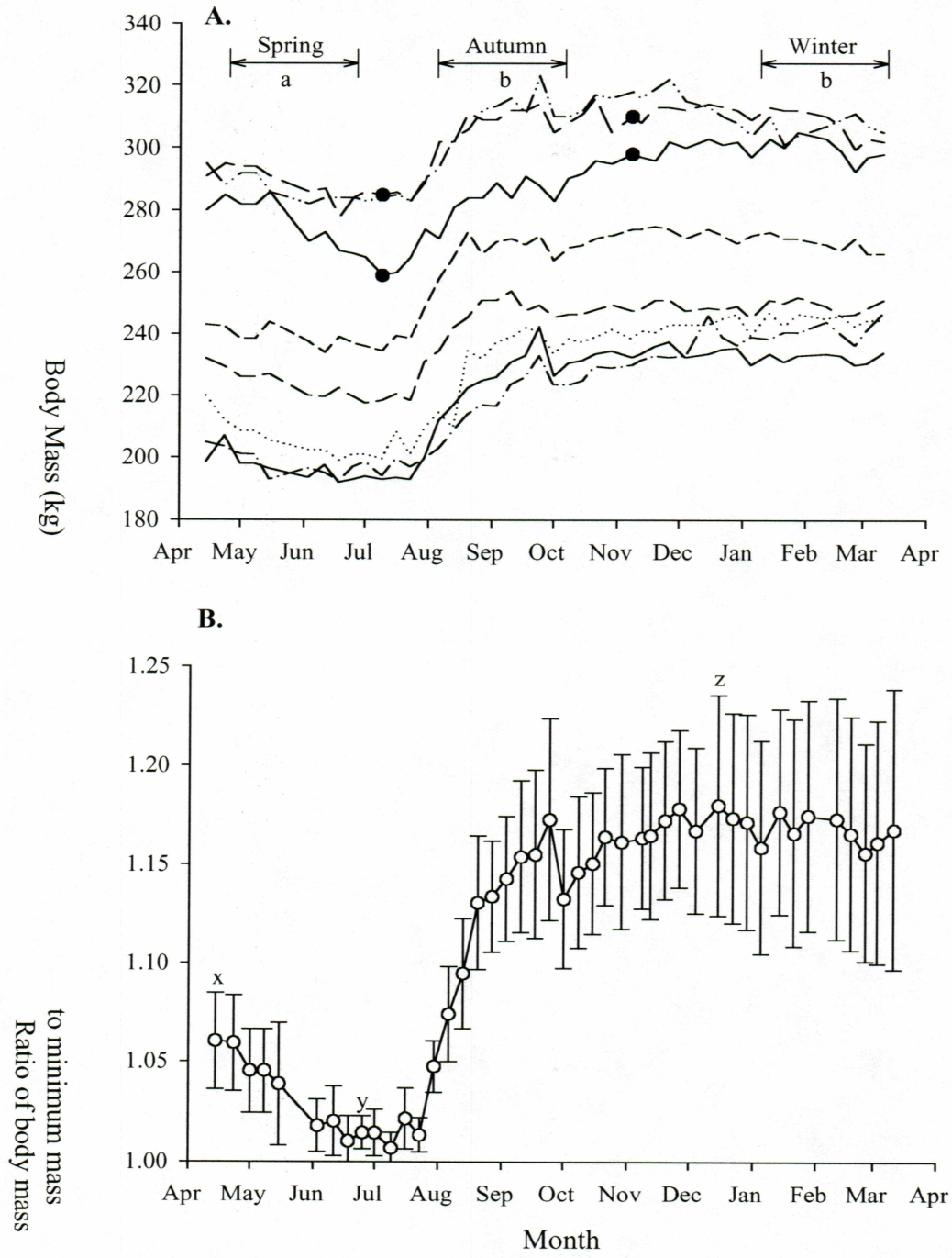

Figure 1.

Figure 2.1 —Weekly Body Mass of Eight Adult Muskoxen

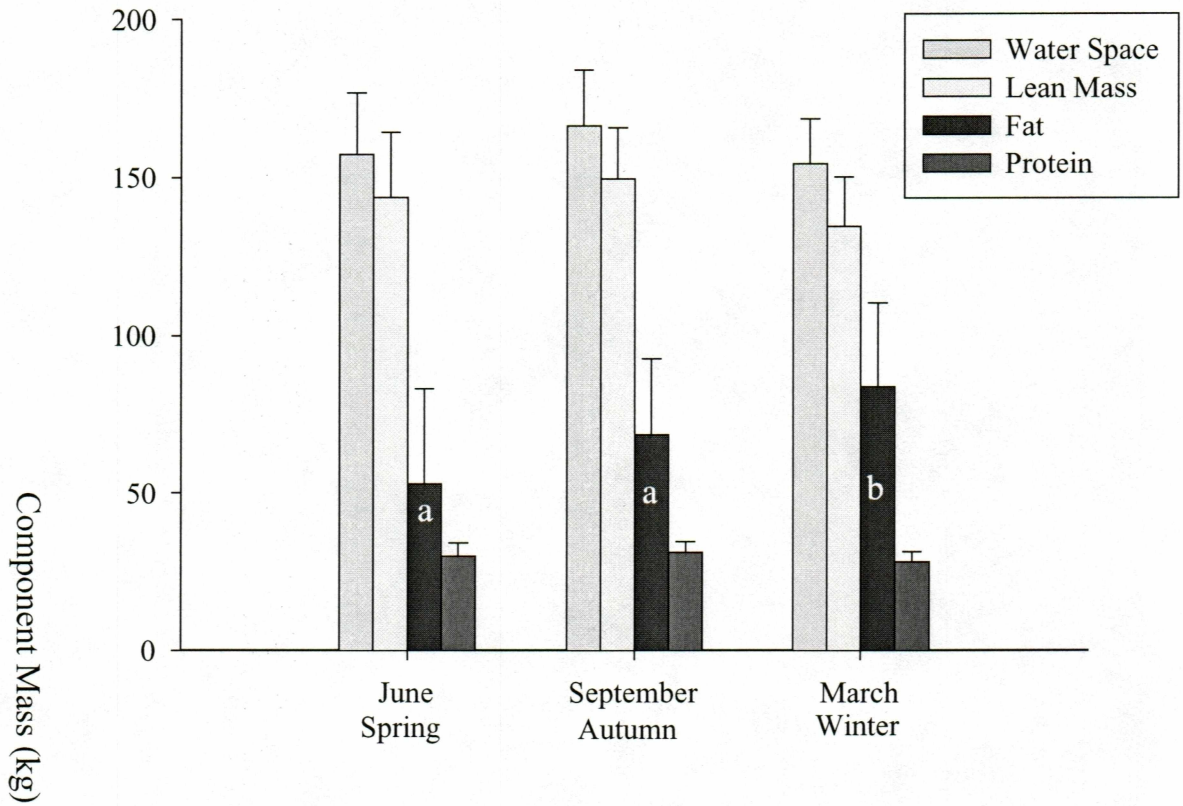

Figure 2.

Figure 2.2 -- Body Composition of Adult Muskoxen Based on Tritium Dilution

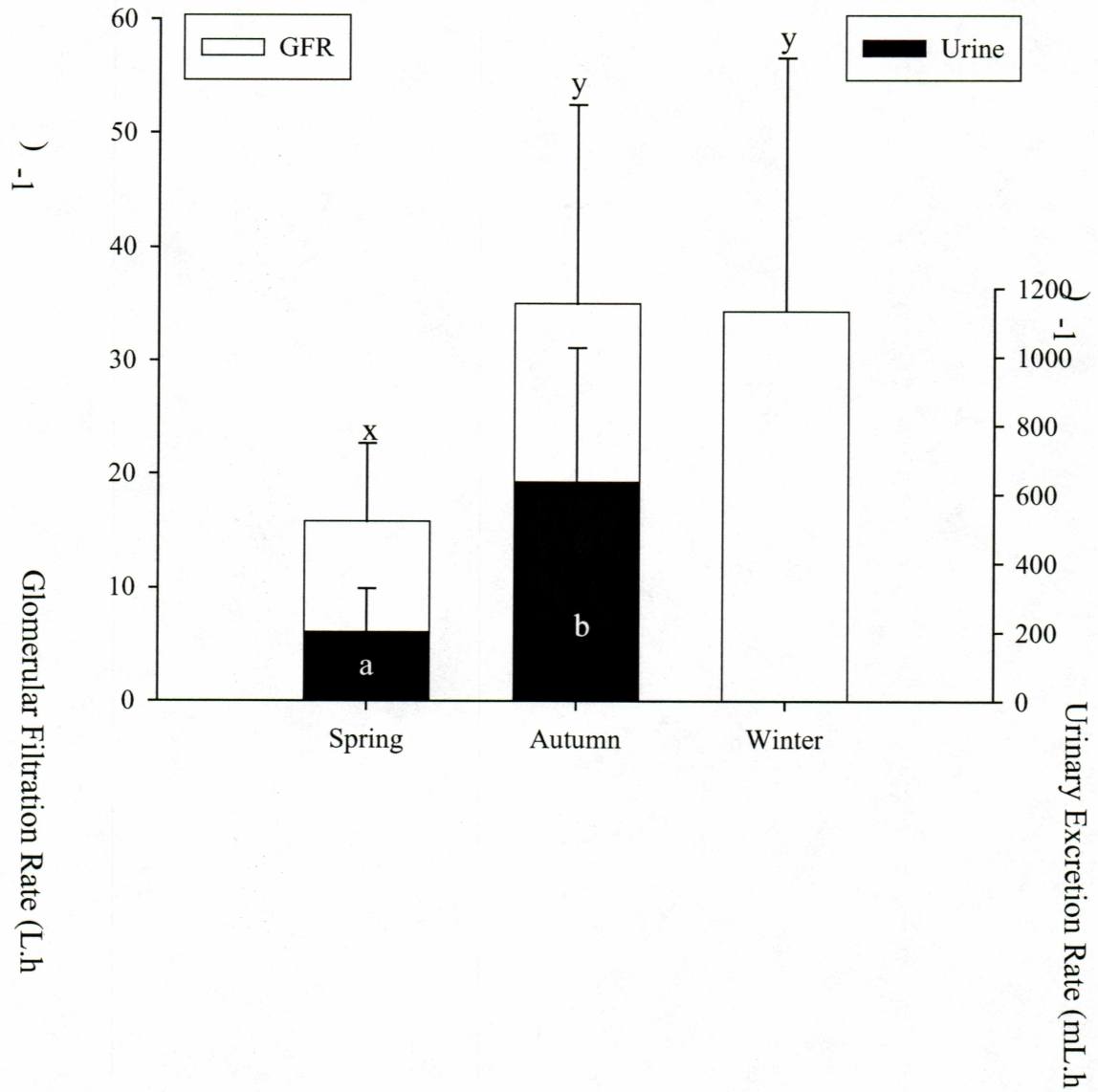

Figure 3.

Figure 2.3 —Glomerular Filtration Rate and Urinary Volume of Adult Muskoxen

CONCLUSIONS

Chapter 1 showed that for growing muskoxen a diet that contains 10% crude protein is sufficient to maintain growth and beyond that level protein supplementation will only result in an increase in temporary fat stores. These stores do not exceed endogenous controls on the system. Another result of this study demonstrated that dimorphic growth is the result of diverging patterns of growth between males and females during autumn. Both the limits of tissue accumulation and the differences related to sex are probably the result of hormonal controls. As a result of these controls, the animals in our study may have been growing at their maximum capacity.

Chapter 2 showed that non-reproductive males gain body mass from spring to winter. The gains are fat and not lean tissue, therefore nitrogen supplementation will not result in lean tissue accumulation in adults. The breakdown of dietary fiber results in the release of digestible energy. As intakes increase, the animal is able to increase its ability to absorb nutrients thus increasing its intake of digestible energy. Cellulose digestibility does not change with intakes from spring to summer but does diminish during winter and suggests seasonal regulation of digestive and absorptive systems. The limitations for growth on high intakes may be in the animals ability to retain electrolytes as excess nitrogen is filtered from the kidneys.

Captive studies such as this one have a limited scope of application to the wild. The animals in this study were not subject to the same conditions as those encountered in the wild. They did not have the same constraints on finding suitable forage, predation avoidance, and reproductive cycles that muskoxen in the circumpolar arctic are subject

to. Nevertheless, these studies should provide value in that they have provided a baseline for comparison to conditions in the wild. We have determined differences in growth rates between males and females and when those differences occur. These differences are innate and therefore would be similar to conditions in the wild. We have determined the role of protein in the growth of these animals in this setting and therefore are able to discern the level of protein needed to meet basic growth requirements in the wild. This does not mean to say that we have determined protein requirements in the wild, because the form of protein found, and the possibility for substances such as secondary compounds in limiting protein uptake, can change the total amount of protein required to meet an animal's needs. These limitations apply to mineral uptake and utilization as well.

The true value of these studies lies in the fact that these sorts of experiments have not been completed before. Other studies have looked at growth, or the use of protein, or the digestibility of different diets, but they have not accounted for the quality of diet, the amount of food ingested, the role of reproductive status, or a combination of these variables. These studies will help differentiate between the roles of nutrition and the endogenous controls of seasonal and absolute growth.

LITERATURE CITED

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